PROCEEDINGS
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# A NEW SPECIES OF *ILLEX* FROM THE WESTERN ATLANTIC AND DISTRIBUTIONAL ASPECTS OF OTHER *ILLEX* SPECIES (CEPHALOPODA: OEGOPSIDA).[1]

By Clyde F. E. Roper,[2] C. C. Lu,[3] and Katharina Mangold[4]

*Introduction*: During the course of an examination of cephalopod specimens of the genus *Illex* from tropical waters of the western Atlantic, two of us (KM and CFER) discovered specimens that did not conform to the characteristics of previously known species. While working at the Smithsonian Institution on a large collection of *Illex* from the Chesapeake Bight region as part of a monographic study on the genus, one of us (CCL) encountered additional specimens of the undescribed species.

Traditionally, two forms of *Illex* have been recognized in the North Atlantic; they have long, though not exclusively, been referred to as subspecies: *Illex illecebrosus illecebrosus* (Lesueur, 1821) in the western Atlantic from northern Brazil, the Caribbean, the Gulf of Mexico, north to Newfoundland and across northern European waters south to Bristol Channel; and *Illex illecebrosus coindetii* (Verany, 1837) in the eastern Atlantic from the British Isles through the Mediterranean and south along the western African coast to Angola. The investigation that led to the discovery of the new species centered around an attempt to establish the taxonomic and distributional relationships of the presumed *Illex illecebrosus illecebrosus* in the tropical western Atlantic to the north Atlantic form of the species and to *I. illecebrosus coindetii* in the eastern Atlantic and

[1] Contribution No. 28 from the Marine Sciences Research Laboratory.

[2] Division of Mollusks, Smithsonian Institution, Washington, D.C. 20560.
[3] Marine Sciences Research Laboratory, Memorial University, St. John's, Newfoundland, Canada.
[4] Laboratoire Arago, Banyuls-sur-Mer, France.

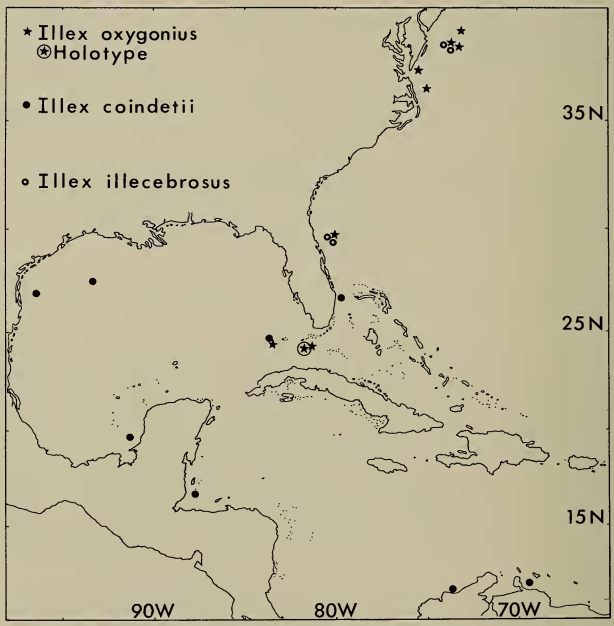


FIGURE 1. Capture-localities of *Illex* species in the middle western North Atlantic.

the Mediterranean. The result of this investigation are reported here: the subspecies of *Illex, I. illecebrosus illecebrosus, I. illecebrosus coindetii,* and the recently established *I. illecebrosus argentinus* (Castellanos, 1960) are demonstrated to have status as full species; the new species is described and compared with the other species of *Illex*; *I. coindetii* is recorded for the first time from the western Atlantic in warm waters; and general distributional ranges are discussed. A full and detailed revision of the systematic and zoogeography of all species of *Illex* is now in progress (CCL).

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*Measurements and Abbreviations*: Most of the measurements (in mm) and indices used in this paper are those commonly used for squid, with dorsal mantle length (ML) the standard against which other measurable characters are compared. Abbreviations of most measurements and indices are presented in Voss (1963). Some additional measurements have been taken to aid in the description of the species and to help define sexual dimorphism. Normally, mantle width (MW) is given as a single value that represents the greatest width of the mantle; in this study three values for mantle width are utilized:

$MW_1$—width at mantle opening

$MW_2$—width at point half-way between anterior insertion of fins and anterior end of mantle (dorsal side)

$MW_3$—width at point in line with anterior insertion of fins

HL—length of head along dorsal midline from posterior ridge to V-shaped juncture between arms I.

The fin angle is the angle that the straight posterior border of

TABLE 1. Measurements (in mm) of *Illex oxygonius* new species

| | *Oregon* | VIMS | VIMS | VIMS | FH | FH | VIMS | *Oregon* | VIMS | VIMS | VIMS |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Sta. No. | 6801 | 167 | 167 | 167 | 7296 | 7281 | 167 | 6801 | 167 | 167 | 167 |
| Sex | ♂ | ♂ | ♂ | ♂ | ♂ | ♂ | ♀ | ♀ | ♀ | ♀ | ♀ |
| DML | 135 | 160 | 176 | 178 | 205 | 207 | 174 | 181 | 184 | 196 | 210 |
| VML | 120 | 144 | 172 | 166 | 192 | 200 | 174 | 174 | 176 | 189 | 210 |
| $MW_1$ | 26 | 27 | 32 | 34 | 39 | 39 | 31 | 29 | 33 | 33 | 37 |
| $MW_2$ | 22 | 22 | 23 | 30 | 32 | 31 | 30 | 28 | 29 | 30 | 39 |
| $MW_3$ | 15 | 13 | 19 | 18 | 19 | 19 | 22 | 17 | 18 | 21 | 30 |
| FL | 60 | 69 | 74 | 80 | 92 | 94 | 79 | 77 | 83 | 84 | 95 |
| FW | 70 | 70 | 84 | 90 | 99 | 98 | 99 | 78 | 91 | 99 | 107 |
| Fin angle | 35° | 30° | 33° | 31° | 27° | 28° | 38° | 27° | 34° | 34° | 30° |
| HL | 25 | 27 | 29 | 35 | 33 | 31 | 28 | 26 | 29 | 26 | 39 |
| HW | 27 | 33 | 33 | 36 | 47 | 44 | 33 | 29 | 32 | 33 | 41 |
| $A_I$ | 56 | 58 | 62 | 74 | 87 | 88 | 65 | 51 | 58 | 57 | 74 |
| $A_{II}$ | 68 | 72 | 86 | 96 | 109 | 108 | 78 | 66 | 71 | 68 | 94 |
| $A_{III}$ | 68 | 70 | 88 | 97 | 103 | 108 | 74 | 66 | 70 | 72 | 98 |
| $A_{IV}$ (normal) | 62 | 63 | 79 | 80 | 92 | 88 | 70 | 58 | 65 | 64 | 83 |
| $A_{IV}$ (hect.) | 75 | 65 | 85 | 90 | 103 | 103 | | | | | |
| Length of hect. portion | 22 | 20 | 26 | 27 | 32 | 33 | | | | | |
| TL | 115 | 115 | — | 112 | 120 | 125 | 108 | 121 | 112 | 104 | 135 |
| CL | 54 | 54 | — | 51 | 53 | 61 | 47 | 58 | 50 | 47 | 61 |
| $S_I$ | 1.9 | 2.1 | 2.7 | 3.1 | 3.0 | 3.0 | 2.3 | 2.0 | 2.3 | 2.2 | 2.8 |
| $S_{II}$ | 3.5 | 3.6 | 4.0 | 4.5 | 5.2 | 5.0 | 3.2 | 3.5 | 3.2 | 3.1 | 4.3 |
| $S_{III}$ | 3.5 | 3.5 | 4.0 | 4.5 | 5.0 | 5.0 | 3.2 | 3.4 | 3.0 | 3.1 | 4.1 |
| $S_{IV}$ | 1.9 | 1.9 | 2.5 | 2.7 | 2.8 | 2.7 | 2.1 | 1.9 | 2.2 | 2.0 | 2.6 |
| $S_{IV}$ (hect.) | 1.7 | 1.9 | 2.3 | 2.7 | 2.8 | 2.4 | | | | | |
| $S_{Club}$ | 2.3 | 2.5 | — | 3.4 | 4.0 | 4.0 | 2.9 | — | 2.7 | 2.9 | 4.0 |
| Hect. arm | L | L | L | L | R | L | | | | | |
| Nid. gl. | | | | | | | 96 | 76 | 23 | — | 106 |

one fin, exclusive of the lateral lobe, makes with the longitudinal axis (mid-dorsal line) of the body.

Table 1 lists the measurements of *Illex oxygonius*, and Table 2 presents the ranges and means of the indices.

Several abbreviations of ships and institutions are used in reference to specimens:

FH *Fish Hawk*
G *Grampus*
O *Oregon*
VIMS Virginia Institute of Marine Science

Family OMMASTREPHIDAE Steenstrup, 1857
Genus *Illex* Steenstrup, 1880
Type species: *Illex illecebrosus* (Lesueur, 1821).

**Illex oxygonius**, new species
Plates 1–5, 10A

LIST OF MATERIAL

| Sex | ML, mm | Station | Location | Date | Depth, m |
|---|---|---|---|---|---|
| Holotype: | | | | | |
| ♂ | 207 | FH 7281 | 24°13′N 81°58′W | 14 II 1902 | 555 |
| Paratypes: | | | | | |
| ♂ | 205 | FH 7296 | 24°22′N 81°48′W | 26 II 1902 | 222 |
| ♂ | 160 | VIMS 167 | 38°27′N 73°23′W | 25 VIII 1967 | 190 |
| ♂ | 135 | O 6801 | 29°39.5′N 80°08.5′W | 20 VII 1967 | 383 |
| ♀ | 181 | O 6801 | 29°39.5′N 80°08.5′W | 20 VII 1967 | 383 |
| ♂ | 176 | VIMS 167 | 38°27′N 73°23′W | 25 VIII 1967 | 190 |
| ♀ | 210 | VIMS 167 | 38°27′N 73°23′W | 25 VIII 1967 | 190 |
| Other material: | | | | | |
| ♂ | 228 | G-line 2 | 38°52′N 72°58′W | 8 X 1892 | 155 |
| ♂ | 178 | VIMS 167 | 38°27′N 73°23′W | 25 VIII 1967 | 190 |
| ♀ | 174 | VIMS 167 | 38°27′N 73°23′W | 25 VIII 1967 | 190 |
| ♀ | 184 | VIMS 167 | 38°27′N 73°23′W | 25 VIII 1967 | 190 |
| ♀ | 196 | VIMS 167 | 38°27′N 73°23′W | 25 VIII 1967 | 190 |
| ♂ | 170 | VIMS 188 | 36°18′N 74°52′W | 31 VIII 1967 | 68 |
| ♀ | 181 | VIMS 177 | 37°22′N 74°47′W | 27 VIII 1967 | 50 |
| ♂ | 164 | VIMS 166 | 38°34′N 73°33′W | 25 VIII 1967 | 73 |
| ♀ | 136 | O 1011 | 24°28′N 83°25′W | 14 IV 1954 | 364 |

*Diagnosis*: Fin angle acute (25°–35°); fin width equal to fin length; mantle narrow, drawn out posteriorly; dorsal mantle lobe conspicuous, pointed in males; hectocotylized portion of arm IV long, 3 papillae on dorsal row; cone at oral end of cement body of spermatophore funnel-shaped.

*Description*: *Mantle* long, slender, broadest anteriorly, drawn out posteriorly into long attenuate tip (pl. 1A). Mantle width decreases markedly posteriorly in males, less so in females especially at maturity (Table 2). Ventro-lateral lobes on mantle opening inconspicous, rounded; dorsal lobe conspicuous, pointed (pl. 1B). Thin, membranous flange encircles mantle opening. Mantle wall thin for an ommastrephid. *Fins* narrow, drawn out to acute point posteriorly; width (48–50 percent of ML) about equal to length (44 percent of ML); ratio of length to width = 1:1.01 to 1:1.25; slightly concave posterior borders form acute angle of 25°–35° (average about 30° in males, 32° in females); lateral borders rounded; anterior lobes well developed (pl. 1B).

TABLE 2. Ranges and means of indices of *Illex oxygonius* new species (n = 11; 6 males, 5 females)

| | Males | | Females | |
|---|---|---|---|---|
| | Mean | Range | Mean | Range |
| $MW_1I$ | 18.3 | 17–19 | 17.4 | 16–18 |
| $MW_2I$ | 15.2 | 13–17 | 16.4 | 15–19 |
| $MW_3I$ | 9.7 | 8–11 | 11.4 | 9–14 |
| HLI | 17.1 | 15–20 | 15.6 | 13–19 |
| HWI | 20.7 | 19–23 | 17.8 | 16–20 |
| FLI | 44.0 | 42–45 | 44.2 | 43–45 |
| FWI | 48.2 | 44–52 | 50.4 | 43–57 |
| FL/FW | 1/1.10 | 1/1.01–1/1.17 | 1/1.13 | 1/1.01–1/1.25 |
| Fin angle | 30.7 | 27–35 | 32.6 | 27–38 |
| $A_II$ | 39.8 | 35–43 | 32.2 | 29–37 |
| $A_{II}I$ | 50.5 | 45–54 | 40.0 | 35–45 |
| $A_{III}I$ | 50.2 | 44–55 | 40.2 | 36–47 |
| $A_{IV}I$ | 43.9 | 39–46 | 36.0 | 32–40 |
| $A_{IV}$ (hect.) I | 49.3 | 41–56 | | |
| Hect. portion percent of arm | 30.8 | 29–33 | | |
| $S_II$ | 1.49 | 1.31–1.74 | 1.20 | 1.10–1.33 |
| $S_{II}I$ | 2.41 | 2.25–2.59 | 1.83 | 1.58–2.05 |
| $S_{III}I$ | 2.39 | 2.19–2.59 | 1.77 | 1.58–1.95 |
| $S_{IV}I$ | 1.37 | 1.19–1.52 | 1.14 | 1.02–1.24 |
| $S_{Hect.}I$ | 1.30 | 1.16–1.52 | | |
| $S_{Club}I$ | 1.81 | 1.56–1.95 | 1.63 | 1.47–1.90 |

*Funnel* well developed, set in deep funnel groove; lateral adductor muscles conspicuous, strong, rodlike (pl. 1A); anterior adductors thin, broad, sheetlike. Dorsal *funnel organ* large (pl. 3A); posterior limbs fleshy, thickened, broad anteriorly, tapered, bluntly pointed posteriorly; lateral shoulders conspicuous; anterolateral borders concave; apical papilla spear-head shaped. Sharp, thin ridges extend from anterior mid-portion of limbs nearly to apex. Ventral pads oblong; lateral borders strongly curved; medial borders nearly straight. Funnel valve broad.

*Funnel locking-cartilage* large, strong, inverted T-shaped (pl. 2B). Medial, longitudinal groove narrow, relatively shallow; groove deepens and widens posteriorly to form deep, broad pit. Strongly developed cartilaginous knobs converge, nearly meet posterior to deep pit; lateral knob rounded, medial knob more pointed with narrow ridge extending dorsally into pit; pit undercuts anterior walls of knobs. Groove between knobs narrow, relatively deep, opens into lateral groove. Lateral groove very broadly inverted V-shaped, deepest anteriorly against posterior walls of knobs, shallows along posterior margin of locking-cartilage. Entire cartilage bordered by thin, muscular flange. *Mantle locking-cartilage* (pl. 2C) strong, compliment of funnel lock. Longitudinal ridge low, nar-

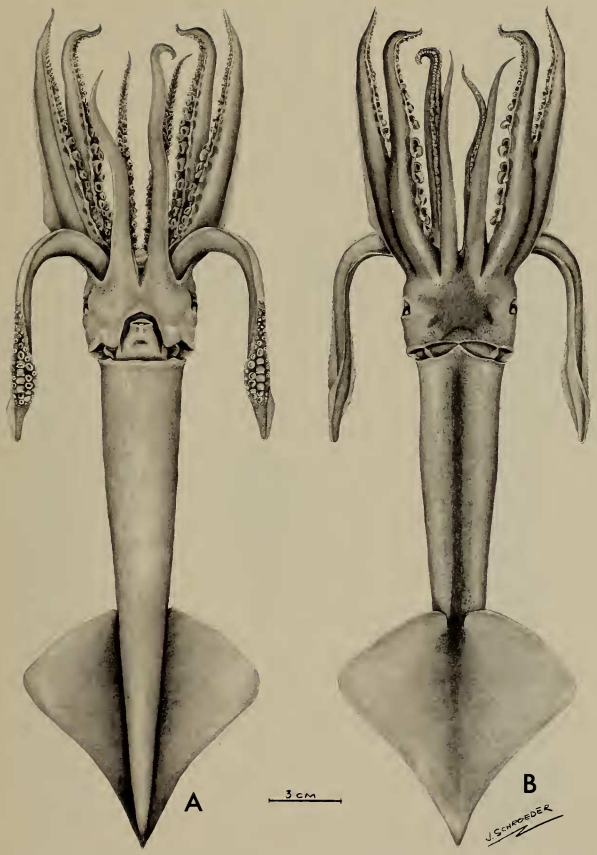



PLATE 1. *Illex oxygonius* new species, Holotype, FH 7281, male, 207 mm ML. A. Ventral. B. Dorsal.

row anteriorly, expands to large, sharply defined, swollen bulb posteriorly; posterior wall very deeply undercut toward base on mantle. Thin ridge extends from bulb to lateral ridge. Lateral ridge narrow, open V-shaped; anterior walls drop sharply into open grooves, posterior walls taper to mantle wall.

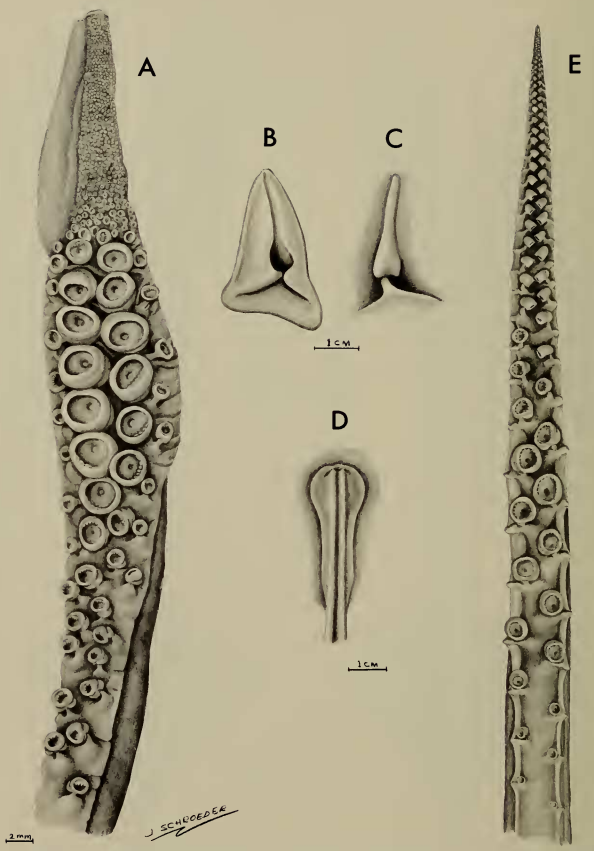



Plate 2. *Illex oxygonius* new species, Holotype. A. Left tentacular club. B, C. Funnel and mantle components of locking cartilage. D. Nuchal locking cartilage. E. Right arm III.

*Head* large, broad, width about 20 percent of ML in males, 17 percent in females; length about 17 percent in males, 15 percent in females. Three flaplike nuchal folds present; nuchal cartilage long, broad and rounded anteriorly, narrow, tapered posteriorly, terminally embedded in muscle;

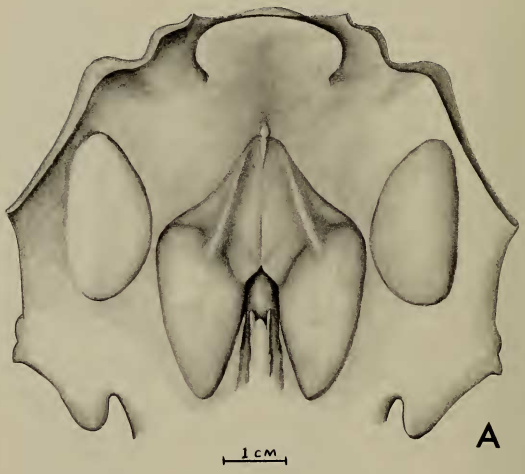
central groove deep, lateral ridges distinct (pl. 2D). Eye openings subcircular, dorsoventrally elongate; anterior sinus deep, conspicuous.

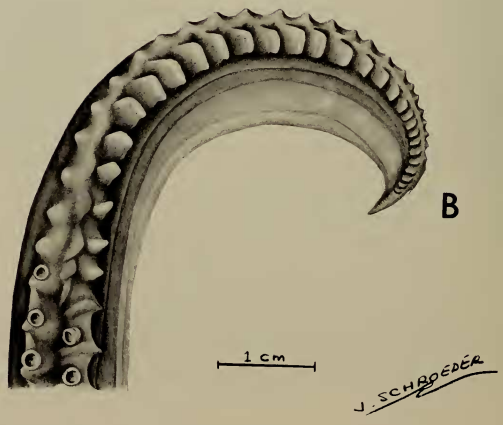
*Arms* long, attenuate; order $2 \geqslant 3 > 4 > 1$; longer in males than in females, especially II and III (Table 1); arms II, III robust; IV less robust; I least robust, very slender (pl. 1A, B). Swimming keels very low, weak on distal half of I; higher, better developed, full length of II; best developed on III, broadest in proximal quarter; low, second best developed, full-length of IV. Protective membranes well-developed, particulary ventral membranes; trabeculae long, very strong, arise from base of sucker stalks, form high points along membranes. Suckers of arms larger in males than in females, especially on II and III (Table 2). Suckers small on I and III; about 6 pairs enlarged on II and III of male (pl. 2E).

*Arm sucker dentition.* Largest rings of Arm I (pl. 4A) with low, broad plate on proximal 1/3, 3–5 low, truncate or slightly rounded teeth laterally, becoming narrower, longer distally; distal median tooth enlarged, elongate, more pointed; teeth, especially median tooth, more truncate, blunt on basal sucker pairs, more pointed on distal pairs. Largest rings of II (pl. 4B) with 2 low, broad, flat teeth proximally, 5–7 teeth laterally, broader, more truncate proximally, narrower, more rounded distally; distal median tooth greatly enlarged, triangular, pointed. Smaller rings smooth proximally and with fewer teeth, 5–6 long, narrow teeth distally, grade in size to median tooth. Ring dentition of III about as II; broad, low single or bifurcate plate proximally, 5–7 lateral teeth graded distally, median tooth very enlarged, elongate, pointed (pl. 4C). Smaller rings with broad, low plates proximally, 1–2 rounded teeth laterally, 2–3 long pointed teeth laterally graded to longest median tooth. Largest rings of IV with broad, low proximal plate, 3–5 rounded to truncate lateral teeth (may be longer, narrower distally), elongate bluntly pointed or rounded distal median tooth.

Left or right ventral arm *hectocotylized* (pl. 3B), longer (average about 6 percent), more robust than non-hectocotylized arm IV; modified tip 29–33 percent (average 31 percent) of arm length; distal suckers reduced in size, rows separated. Suckers of dorsal row give way to 3 conical papillae; remnant of protective membrane disappears distal to third papilla; next distal 1–2 protuberances become flattened, followed by series of transversely broad, thin, nearly truncate flaps; flaps gradually reduced in size distally, finally giving way at arm tip to series of minute papillae (28 recognizable flaps on holotype–exclusive of proximal 3 papillae and 9 distal precursors). Suckers of ventral row give way to conical, nipple-like papillae that extend, gradually reduced in size, to tip of arm (42 papillae in holotype). Low, weak zigzag ridge between papillae and flaps. Aboral keel broadly expanded along modified portion of hectocotylus tip. Trabeculae not modified as fringed lobes.

*Tentacles* robust, relatively short; stalks naked. Clubs expanded, long, about 28–30 percent of ML (pl. 2A). Distinct carpal cluster absent; suckers in carpal area small, biserial; carpal knobs lacking. Manal suckers tetraserial; suckers on lateral rows small; medial sucker rows arise distal


1 cm
A


B
1 cm
J. SCHROEDER

to the proximal 5 carpal suckers; proximal 3–5 medial suckers small, gradually increasing in diameter; about 15 medial suckers on manus greatly enlarged; maximum size greater in males than in females; manus terminates abruptly. Dactylus distinct, slender; suckers in 8 or 9 rows, extremely numerous, minute; suckers near tip slightly enlarged; tip with narrow, suckerless flange. Swimming keel along entire tentacular stalk aborally, broadest proximal to club, diminishes along carpal and manal region, expands to broad keel along dactylus. Lateral angles distinct on oral surface of stalk and continue as broad heavily supported protective membranes along club, diminish significantly along dactylus. Dual V-shaped trabeculae arise from enlarged common base with lateral suckers along manus.

*Club sucker dentition.* Sucker rings of carpal area with low, broad plate on proximal half, 4–6 small teeth on distal half; lateral teeth broad, rounded; distal teeth narrow, bluntly pointed. Proximal-most lateral manal suckers with proximal plate, 1–2 low, rounded lateral teeth, 4–7 long, narrow pointed distal teeth; distal lateral suckers toothed around entire margin with 5–8 low, rounded proximal teeth, 12–14 longer, sharply pointed lateral and distal teeth, occasional small pointed secondary tooth between primary teeth. Proximal medial manal suckers (first 5–7) with low proximal plate, 1–2 low, rounded, lateral teeth, 1–2 slightly narrower distolateral teeth, 1 buntly pointed median tooth; next distal 4–5 enlarged sucker rings with 7–13 teeth around margin—low, flat proximally, narrow, rounded distally, no enlarged or pointed medial tooth (pl. 4E). Dentition lacking, rings entire on 7–8 distal enlarged manal suckers. Proximal dactyl sucker rings with 4–6 long pointed distal teeth; teeth become more blunt, rounded on rings of middle dactylus suckers; teeth on suckers at distal tip few, minute.

*Gladius* (pl. 5A) long, slender, bluntly pointed anteriorly; median ridge and heavy lateral rods extend length of rhachis, converge posteriorly, fuse near vane, continue to tip. Vane short, narrow; forms short, hollow conus; only extreme tip solid.

*Connectives* of buccal membrane attach to dorsal, dorsal, ventral, dorsal borders of arms I–IV respectively.

*Beaks* (pl. 4G, H). Rostrum of upper beak strong, sharp, long, heavily pigmented; dorsal hood very weak, thin, short, lightly pigmented; notch and slight ridge separate rostrum and rostral lamella; cutting edge of rostral lamella straight or slightly curved, smooth; palatine lamella large, long, deep, pigmented anteriorly, dorsal crest only slightly curved. Rostrum of lower beak relatively long, pointed, heavily pigmented, inner edge curved; rostral lamellae narrow, short, wing lobate, thin; gular lamellae large, crest strong, posterior corner long, pointed, curved; rostral width broad.

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PLATE 3. *Illex oxygonius* new species. A. Open funnel showing funnel organ and funnel valve. Holotype. B. Hectocotylus, right arm IV. Paratype, FH 7296, male, 205 mm ML.

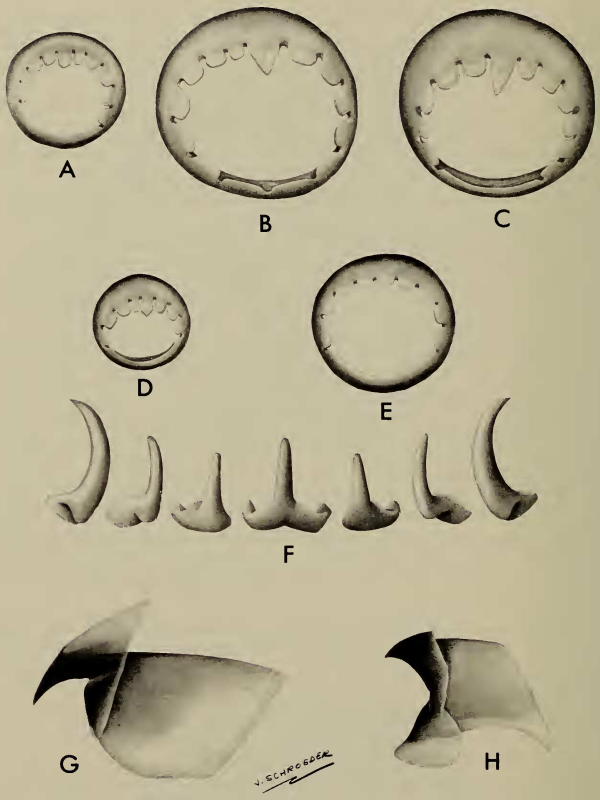



Plate 4. *Illex oxygonius* new species. A-E. Sucker rings from arms I-IV and manus of club, respectively. Holotype. F. Radula, G. Upper beak, H. Lower beak. Paratype, FH 7296.

*Radula* (pl. 4F) with 7 transverse rows of teeth; rhachidian with long central tooth, blunt lateral cusps; first lateral tooth with blunt lateral cusp; second lateral tooth curved, no lateral cusp; third lateral tooth long, curved, scythe-shaped; marginal plaques lacking.

*Spermatophore* (pl. 5B-D, pl. 10A) with sperm mass of about 60 percent of total length, cement body about 15 percent of total length. Cone at

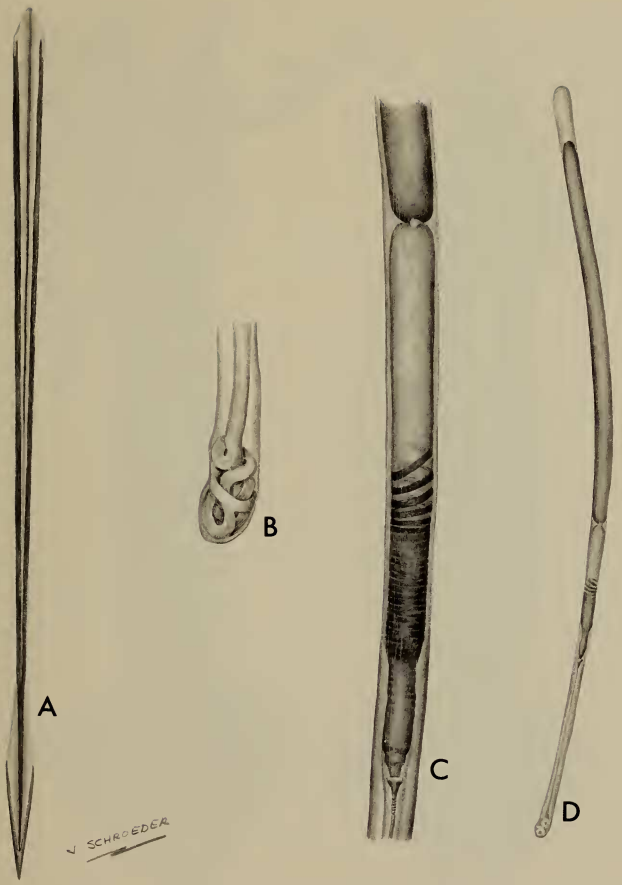



Plate 5. *Illex oxygonius* new species. Paratype, VIMS 167, males, 176 mm ML. A. Gladius. B–D. Spermatophore. B. Oral end. C. Mid-section; cement body ejaculatory apparatus. D. Entire spermatophore.

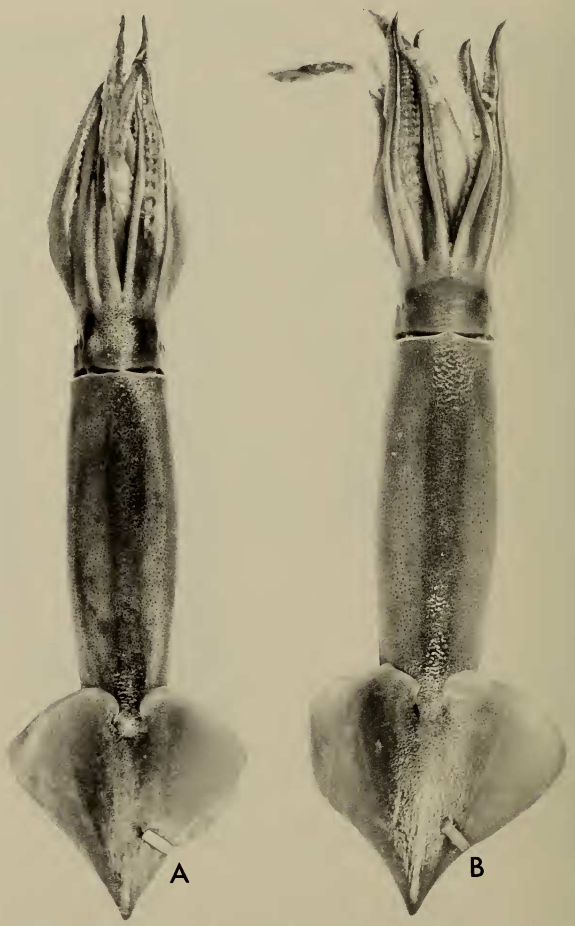



PLATE 6. *Illex illecebrosus* (Lesueur, 1821). A. Male, 252 mm ML. B. Female, 268 mm ML. Newfoundland (from Mangold, et al., in press).


PLATE 7. *Illex coindetii* (Verany, 1837) A. Male, 166 mm ML. B. Female, 95 mm ML. Western Mediterranean (from Mangold, et al., in press).


PLATE 8. *Illex argentinus* (Castellanos, 1960). A. Female, 187 mm ML. B. Male, 172 mm ML Argentina.

oral end of cement body funnel-shaped, connected aborally by short neck; oral tube relatively wide.

*Color* (in isopropyl alcohol). Reddish-brown chromatophores cover entire body, more widely spaced ventrally, thickly packed dorsally; deep purple-red stripe along dorsal mid-line of mantle.

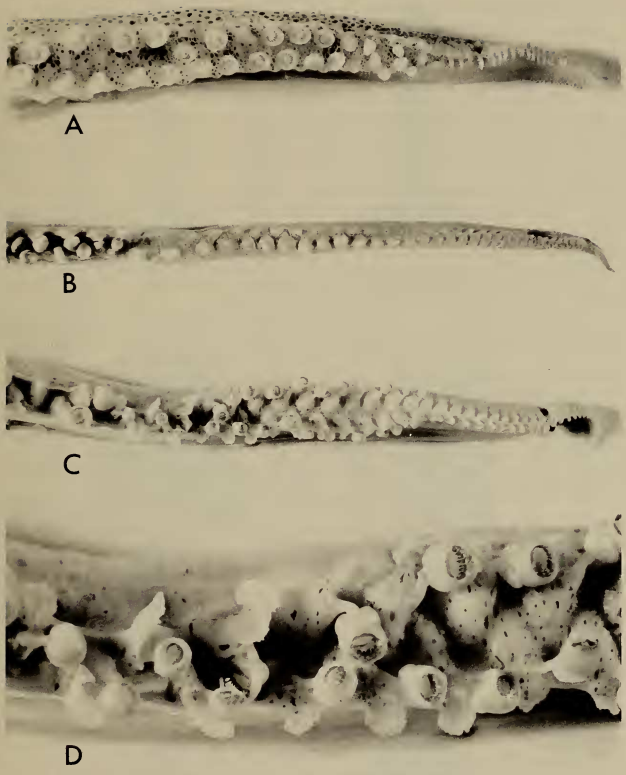
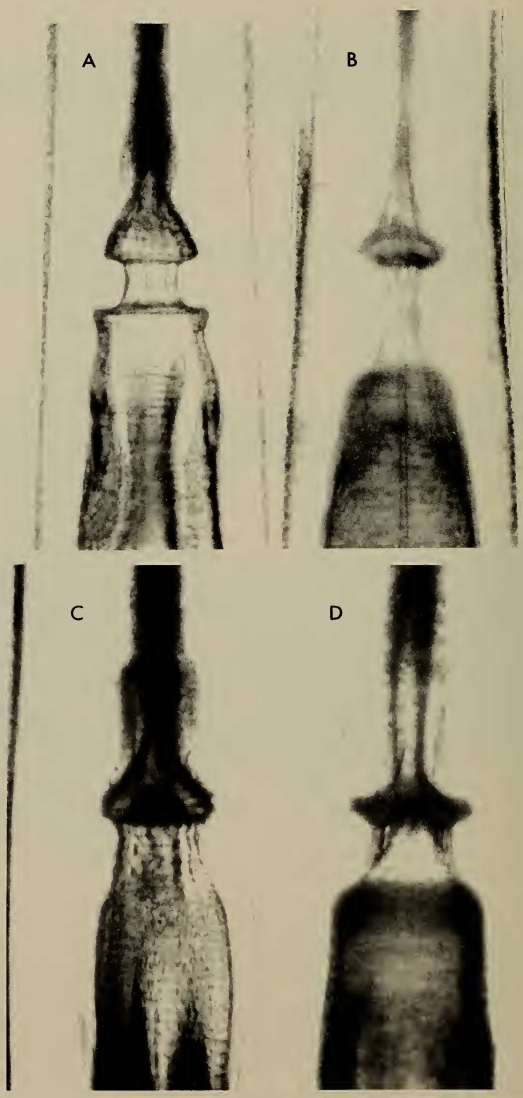



PLATE. 9. Hectocotyli of *Illex* species. A. *I. illecebrosus,* 252 mm ML; Newfoundland. B. *I. argentinus,* 167 mm ML; Argentina. C. *I. coindetii,* 166 mm ML; western Mediterranean. D. *I. coindetii,* enlargement of a portion of C. showing fringed trabeculae.

*Holotype*: United States National Museum (577000).

*Type locality*: 24°13′N 81°58′W in Florida Current about 22 nautical miles SSW of Key West, Florida; *Fish Hawk* station 7281, 14 February 1902, 555 m.

*Distribution*: Western Atlantic: off Middle Atlantic States, Florida Current, Gulf of Mexico (fig. 1). Taken in bottom trawls at depths of 50–555 m.


A
B
C
D

*Etymology*: The name of the species is derived from the Greek word "oxygonios" meaning acute angled. This term refers to the acute angle of the fins in *I. oxygonius*.

*Discussion*: *Illex oxygonius*. *Illex oxygonius* exhibits a considerable sexual dimorphism in several characters (Table 2). The width of the mantle in males decreases sharply posteriorly, while that of females decreases gradually; this gives females a fuller, more robust appearance along the middle and posterior portions of the mantle. Head size differs between sexes; males have longer, wider heads than females. Fin width in females tends to be slightly wider than in males; this results in a slightly greater fin angle. All arms in males are longer than the corresponding arms in females; arms II and III are especially more elongate and more robust. The maximum size of suckers on all arms, particularly on arms II and III, is greater in males than in females. Males have larger tentacular club suckers than do females.

While few specimens are currently available, it appears that *I. oxygonius* generally may inhabit depths greater than around 100–200 m, particularly in lower latitudes where it is recorded from 222 to 555 m.

All males of *I. oxygonius* available are mature with completely developed hectocotyli and Needham's sacs filled with completely formed spermatophores; males range from 135–228 mm in ML. At least some females become fully mature by 174 mm ML with swollen nidamental glands of 96 mm length and completely filled ovaries.

*Comparison of species*. Steenstrup (1880) erected the genus *Illex* to encompass two distinct species, *I. illecebrosus* (Lesueur, 1821) and *I. coindetii* (Verany, 1837). Pfeffer (1912) had access to a large collection of *Illex* from a number of localities in the Atlantic; he formed the opinion that *illecebrosus* and *coindetii* were subspecies. Pfeffer's subspecific designations have been followed since (e.g., Degner, 1925; Grimpe, 1921, 1924, 1925; Adam, 1939, 1952). Acceptance of the subspecies concept, however, has not been universal (Naef, 1916, 1921, 1923; Voss, 1956; Clarke, 1966).

The taxonomic problems in the genus *Illex* have been further complicated by the absence of holotypes. In fact, no type specimen was kept for *illecebrosus* by Lesueur (1821), and the type of *coindetii* is no longer extant (Voss, 1962). Castellanos (1960) described a new species called *Ommastrephes argentinus* which was later placed in *Illex* as the third subspecies of *illecebrosus* (Castellanos, 1964).

The comparisons of species are based on a large sample of specimens of *Illex* from various localities. Specimens of *illecebrosus* have been examined and confirmed as conspecific from Newfoundland, and Labrador, Gulf of Maine, Middle Atlantic States, and off north Florida. Specimens

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PLATE 10. Spermatophores of *Illex* species. A. *I. oxygonius*. B. *I. illecebrosus*. C. *I. coindetii*. D. *I. argentinus*.

of *coindetii* come from the Mediterranean, Gulf of Guinea, West Africa, Gulf of Mexico and the Caribbean; we have examined and compared the specimens from these areas and have concluded that they are conspecific.

*Illex oxygonius* may be distinguished from other species of *Illex* by a number of characters. Information on distinguishing characteristics has been accumulated from a large sample of specimens of *illecebrosus* and *coindetii* from the North Atlantic; information on *argentius* from South American waters, however, is available from only eleven specimens of which data from eight were presented in Mangold, et al. (in press). Several of the characters are presented as indices of morphometric features; the mean values are given followed by the ranges in parentheses. In general, the indices tabulated are of *illecebrosus* from Newfoundland and of *coindetii* from the western Mediterranean (Mangold, et al., in press), but other characters used include, in addition, *illecebrosus* from the Chesapeake Bight region and *coindetii* from West Africa, the Gulf of Mexico and Caribbean. Males and females of *illecebrosus*, *coindetii* and *argentinus* are illustrated in plates 6–8 respectively.

*Head width.* The head width of *oxygonius* in general is greater than that of other species, with the exception of the male of *coindetii*. The males of *oxygonius* have an average head width index of 20.7 (19–23), of *illecebrosus* 15.2 (14.5–17.1), of *coindetii* 20.0 (17–22.4), and of *argentinus* 15.9 (13.0–18.6); the values for females are, respectively: 17.8 (16–20); 14.9 (13.8–16.6); 15.5 (15.0–16.2); 14.3 (12.4–16.1). Sexual dimorphism in head width occurs in all species except *illecebrosus*.

*Arms.* Males and females of *oxygonius* have the smallest indices of all arms of the four species:

| | *I. oxygonius* | *I. illecebrosus* | *I. coindetii* | *I. argentinus* |
|---|---|---|---|---|
| *Male* | | | | |
| Arm I | 39.8(35–43) | 42.8(42.5–42.8) | 54.9(42.2–63.8) | 59.2(57.1–63.0) |
| II | 50.5(45–54) | 51.4(51.8–55.3) | 71.9(55.1–87.7) | 73.0(68.7–77.8) |
| III | 50.2(44–55) | 52.3(50.4–50.6) | 71.4(53.3–87.7) | 72.4(69.4–75.9) |
| IV[1] | 43.9(39–46) | 45.3(43.9–46.2) | 52.4(48.2–77.6) | 63.0(60.1–67.3) |
| *Female* | | | | |
| Arm I | 32.2(29–37) | 38.1(38.3–44.2) | 43.8(39.7–43.7) | 44.1(39.4–47.7) |
| II | 40 (35–45) | 45.3(44.1–55.2) | 56.3(56.2–56.5) | 53.1(48.2–57.0) |
| III | 40.2(36–47) | 46.2(44.1–53.3) | 56.1(55.3–56.6) | 53.2(47.6–56.8) |
| IV | 36 (32–40) | 41.1(41.5–47.3) | 50 (49.2–51.0) | 47.1(41.8–50.0) |

[1] Data for normal arm, not hectocotylus.

The figures show that the males have longer arms than the females, particularly in *oxygonius*, *condetii* and *argentinus*; the sexual dimorphism in arm lengths of *illecebrosus* is less pronounced. Arms II and III of male *oxygonius*, *coindetii* and *argentinus* are more robust than corresponding arms in females; this is especially so in *coindetii*. Arms II and III of male *illecebrosus* are not enlarged. The largest suckers on arms II and III of male

*oxygonius, coindetii* and *argentinus* are conspicuously larger than those in females; no such enlargement occurs in *illecebrosus*:

| | *I. oxygonius* | *I. coindetii* | *I. argentinus* | *I. illecebrosus* |
|---|---|---|---|---|
| *Male* | | | | |
| Arm I | 1.49 (1.31–1.74) | 1.74 (1.28–2.22) | 1.64 (1.58–1.72) | 1.17 (0.93–1.54) |
| II | 2.41 (2.25–2.59) | 3.44 (2.26–4.32) | 3.21 (2.99–3.33) | 1.61 (1.52–1.74) |
| III | 2.39 (2.19–2.59) | 3.29 (2.15–3.99) | 2.97 (2.88–3.07) | 1.62 (1.48–1.79) |
| IV[1] | 1.37 (1.19–1.52) | 1.52 (1.08–2.02) | 1.53 (1.50–1.59) | 0.98 (0.91–1.12) |
| *Female* | | | | |
| Arm I | 1.20 (1.10–1.33) | 1.32 (1.08–1.62) | 1.28 (1.06–1.45) | 1.14 (1.04–1.23) |
| II | 1.83 (1.58–2.05) | 2.06 (1.78–2.54) | 2.01 (1.59–2.18) | 1.64 (1.37–1.82) |
| III | 1.77 (1.58–1.95) | 2.00 (1.67–2.45) | 1.98 (1.53–2.18) | 1.54 (1.31–1.72) |
| IV | 1.14 (1.02–1.24) | 1.15 (1.00–1.27) | 1.15 (0.89–1.32) | 1.06 (0.90–1.29) |

[1] Data for normal arm, not hectocotylus.

*Beaks.* The beaks of the three species differ in a number of features:

| Feature | *I. oxygonius* | *I. illecebrosus* | *I. coindetii* |
|---|---|---|---|
| *Upper beak:* | | | |
| Rostral hood | short, very thin and weak | long, strong | long, strong |
| Outline of rostral lamella | smooth, straight or slightly curved | serrated | smooth |
| Jaw angle | small | large, with tooth | small |
| Rostrum | short | long | long |
| Palatine lamella | long, deep; crest straight | short, shallow; crest curved | short, shallow; crest curved |
| Rostral lamella | long | short | short |
| *Lower beak:* | | | |
| Cutting edge of rostrum | curved, long | straight, short | straight, long |
| Rostral lamella | short, narrow, lobate; irregular outline | long, wide, no lobe; regular outline | long, wide, no lobe; slightly irregular outline |
| Gular lamella | long, pointed | short, blunt | short, blunt |
| Rostral width | wide | narrow | narrow |

*Features of the mantle.* In *Illex oxygonius* and *coindetii* the widest part of the mantle is at the mantle opening except in fully mature females because of the great enlargement of the nidamental glands and ovary. The mantle in *oxygonius* is long and narrow and tapers evenly to a point posteriorly, while that of *condetii* is shorter, proportionally less narrow, and less drawn out posteriorly. In *illecebrosus* the widest point lies about half-way between the insertion of the fins and the mantle opening; the body is more full, robust.

Male *oxygonius* have a sharp triangular dorsal lobe at the mantle opening. While small lobes may be present in some specimens of other species, they are not as distinct.

Thickness of the mantle wall is a difficult character to quantify, particularly because of changes that may occur after spawning, or at time of fixation, but the mantle wall of *oxygonius* appears to be thin in relation to the mantle walls of other species.

*Fin angle.* The angle of the fins in *oxygonius* is acute, each fin forming an angle of primarily 25°–35°, occasionally up to 40°, with the longitudinal axis of the mantle. The fin angle in *illecebrosus* is between 40°–50°, while in *coindetii* it generally exceeds 50°. Three specimens of *argentinus* have fin angles of 42°, 47° (females), and 50° (male). The ratio of fin length to fin width is 1/1.1 in *oxygonius*, 1/1.3 in *illecebrosus*, 1/1.5 in *coindetii*, and 1/1.4 in *argentinus*.

*Hectocotylus.* Hectocotyli of the species of *Illex* show the same basic structure; the tip of either right or left arm IV is modified in a series of lamellae and knobs (pl. 9). The proportional length of the modified section of the arm varies among the four species: *argentinus*, greater than 50 percent (67 percent) of arm length; *oxygonius*, 30–35 percent; *coindetii*, 30–35 percent; *illecebrosus*, 15–25 percent. The hectocotylus of *coindetii*, which is otherwise generally similar to that of *oxygonius*, has lobate trabeculae that are fringed and papillose (pl. 9C, D); this feature is lacking also in *illecebrosus* and *argentinus*. In *coindetii* from African waters the modified trabeculae are larger, more papillose than those on specimens from the Gulf of Mexico and the Mediterranean. The size of the lamellae along the dorsal row of the modified tip varies; *oxygonius* has the largest lamellae, *coindetii* and *argentinus* slightly smaller, and *illecebrosus* smallest. A few knobs or papillae occur along the dorsal row proximal to the fully developed lamellae; *oxygonius* has about 3 knobs and 2 slightly flattened papillae, *illecebrosus* and *coindetii* have 1–2 knobs. *Illex argentinus* has the most distinctive hectocotylus (pl. 9B); dorsal and ventral rows with 8–9 normal suckers proximally; dorsal row continues with 16 enlarged, rounded, suckerless knobs, 18 large distinct lamellae and 6 or more small indistinct lamellae to the tip; ventral row continues with 7 low, suckerless knobs, 8 nipplelike papillae, and 20 or more small, indistinct, narrow lamellae to the tip.

*Spermatophores.* The primary difference in the spermatophores of the four species occurs at the oral end of the cement body and the aboral end of the ejaculatory apparatus (pl. 10). In *oxygonius* (pl. 10A) the cone is funnel shaped and about equal-sided in profile with rounded corners; the oral tube is relatively broad; the aboral neck is intermediate in width and length in comparison with *illecebrosus* and *coindetii*. In *illecebrosus* the cone in profile is a low right-isosceles triangle with rounded corners; the oral tube is narrow; the neck is long and narrow (pl. 10B). In *coindetii* the cone is lens shaped or a rounded triangle or diamond shape in profile; the oral tube is broad; the neck is very short, broad, indistinct (pl. 10C). In *argentinus* the cone is flat, lens shaped; the oral tube is broad; the neck is broad and distinct (pl. 10D).

*Size and maturity.* In species of *Illex* where sufficient material is

available (e.g., *illecebrosus, coindetii* and probably *argentinus*), the females attain a larger maximum size than the males, and, in general, the males mature at a smaller size than the females. Males of *illecebrosus* in Newfoundland waters attain 270 mm ML but become sexually mature between 220–250 mm ML; females reach 310 mm ML but no fully mature specimens have been observed there. In warmer waters *illecebrosus* does not grow as large as in cold waters and it reaches maturity at a smaller size. *Illex coindetii* attains a smaller maximum size than *illecebrosus* and reaches maturity at a correspondingly smaller size. Throughout its geographic range, however, *coindetii* shows variation both in maximum size and in size at maturity.

Studies now in progress on *Illex*, as well as the present analysis of characters, lead to the conclusion that the subspecific designations can no longer be justified. Based on the accumulated evidence, we consider that the differences among *illecebrosus, coindetii, argentinus* and *oxygonius* are significant at the species level and we elevate these taxa to the status of full species.

## ARTIFICIAL KEY TO THE SPECIES OF *ILLEX*

(This key is based on mature specimens.)

1. Hectocotylus greater than 50 percent of total arm length ..... *I. argentinus* (Castellanos, 1960)
   Hectocotylus less than 40 percent of total arm length ..... 2
2. Hectocotylus about 15–25 percent of total arm length; suckers on arms II and III of males not enlarged; head narrow in adult males ..... *I. illecebrosus* (Lesueur, 1821)
   Hectocotylus about 30–35 percent of total arm length; suckers on arms II and III of males enlarged; head broad in adult males ..... 3
3. Fin angle 25°–40°; fin length/fin width index = 1/1.1; cone at oral end of cement body of spermatophore funnel shaped, length of neck about equal to width ..... *I. oxygonius*, n. sp.
   Fin angle greater than 45°; fin length/fin width index = 1/1.5; cone at oral end of cement body of spermatophore lens shaped, length of neck much less than width ..... *I. coindetii* (Verany, 1837)

*Distribution*: *Illex oxygonius* has been captured at localities that range from about 24° to 39° N and from 73° to 84° W (fig. 1). This area includes southern localities in the Gulf of Mexico, the Straits of Florida, and in the region of the Chesapeake Bight (New Jersey to Virginia). The species is sympatric in at least parts of its range with several other species of *Illex*. It overlaps the southern portion of the range of *illecebrosus*, while the southern part of the range of *oxygonius* overlaps with the northern portion of the range of *coindetii*.

*Illex argentinus*, so far as known, occurs along the Argentine coast from about 35° to 47° S and from 52° to 62° W (Castellanos, 1964;

Castellanos and Menni, 1968). Undoubtedly, the species has a broader distribution than is presently recorded, but the proper delineation of its limits await further investigation based on additional collections.

*Illex illecebrosus* is pan-Atlantic in far northern waters from Newfoundland and Labrador (Grimpe, 1925), Greenland (Muus, 1962), Iceland (Bruun, 1945), and northern European waters south to the Bristol Channel (Adam, 1952). In the western Atlantic *illecebrosus* extends southward from Newfoundland and Labrador all along the east coast of North America. Past records of *illecebrosus* from the Gulf of Mexico and Caribbean Sea very possibly are a combination of two species, *coindetii* and *oxygonius*, so can no longer be used as an indication of true species distribution.

Specimens of *illecebrosus* currently available to us come from Newfoundland and Labrador, Gulf of Maine, and along the east coast of the U.S. Among the southernmost records are the following specimens and localities:

*Oregon* 6800, 7 males, 153–175 mm ML, 8 females, 155–202 mm ML, 29°48′N 80°09.5′W, 333 m

*Oregon* 6801, 8 males, 148–170 mm ML, 2 females, 145–205 mm ML, 29°39.5′N 80°08.5′W, 383 m

*Illex coindetii* in the eastern Atlantic extends from reportedly the North Sea, certainly along the coasts of Portugal and west Africa to 14° S (Adam, 1952); it is very common in the Mediterranean (Mangold, 1963) and Adriatic Sea (Gamulin-Brida and Ilijanic, in press). Now *coindetii* is reported for the first time from the western Atlantic waters of the Caribbean Sea and the Gulf of Mexico. Among the specimens that we have verified as *coindetii* from this region are the following:

*Oregon* II 289, 1 male, 135 mm ML, 11°24′N 73°47′W, 273 m

*Oregon* 445, 4 males, 147–157 mm ML, 2 females, 211–217 mm ML, 19°48′N 91°20′W, 25 m

*Oregon* 550, 2 males, 72–81 mm ML, 1 female, 162 mm ML, 26°55′N 96°25.5′W, 228 m

*Oregon* 3634, 1 male, 160 mm ML, 1 female, 215 mm ML, 16°44′N 87°55′W, 346 m

*Oregon* 4410, 1 male, 155 mm ML, 11°52′N 69°27′W, 420 m

*Oregon* 4411, 1 male, 163 mm ML, 11°55′N 69°27′W, 473 m

*Oregon* 4610, 1 male, 160 mm ML, 27°37′N 93°22′W, 364–382 m

Triton Station, 1 male, 110 mm ML, 1 female, 145 mm ML, South of Palm Beach, Florida, in Florida Current.

Tortugas, Florida, 1 female, 173 mm ML, Gulf of Mexico.

*Illex illecebrosus* is predominantly a cold water species, but its extension into southern waters indicates that it may be eurythermal. Although few experimental data are available, Frost and Thompson (1932, 1933, 1934) have shown through an analysis of fisheries records that *illecebrosus* in Newfoundland waters tolerates a temperature range of 0°–15° C,

but optimal temperatures for maximum catches were 7°–15°; Squires' (1957) data confirm this temperature range. In southern waters *illecebrosus* must survive warmer temperatures if it occurs at shallow depths; however, our southernmost records, O 6800 and O 6801, are from 333–383 m where the temperature is 9°–10°C. The vertical ranges of the western Atlantic species of *Illex* have yet to be determined, consequently little can be stated about temperature and depth relationships.

*Illex coindetii* in the western Mediterranean ranges from about 40–500 m and meets temperatures of 12.5°–20°C (Mangold, 1963). In West African waters *coindetii* was collected between 50–500 m where temperatures ranged from 7.8°–22.7°C (Adam, 1952). Generally similar temperatures occur in the western Atlantic range of *coindetii*.

*Illex argentinus* is captured at depths of 7–800 m where temperatures range from 5°–12°C (Castellanos, 1964; Castellanos and Menni, 1968).

*Illex oxygonius* is recorded from depths of 50–555 m and from temperatures of 7°–13°C.

The complexities of the *Illex* species systematics and distributions that have been discovered during the present study, particularly in the Caribbean, Gulf of Mexico and Atlantic waters from Florida to the Chesapeake Bight, make it difficult at present to establish with certainly the southern limits of the ranges of *illecebrosus, coindetii* and *oxygonius* and the northern limits of *coindetii* and *oxygonius*. Examination of existing collections and systematic sampling for additional material, particularly from western Atlantic warm waters, are required to resolve the systematic and zoogeographical problems that presently preclude a complete understanding of the polytypic genus *Illex*.

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